SPACING BEHAVIOR AND REPRODUCTIVE ECOLOGY OF THE SEMIPALMATED PLOVER AT CHURCHILL, MANITOBA

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ABSTRACT.—We documented solitary and aggregative spacing patterns in Semipalmated Plovers (*Charadrius semipalmatus*) near Churchill, Manitoba. Pairs nesting on gravel directly on the coast nested in larger aggregations and closer to other pairs than inland pairs. Coastal areas were similar to inland areas in (1) density of birds, (2) available gravel nesting habitat, and (3) climatic conditions. The number of pairs per gravel area deviated significantly from that expected from a Poisson distribution. Inland nests were significantly uniform in distribution, whereas coastal nests were distributed randomly among four sites. In 1988, pairs nesting on the coast also nested later and had heavier eggs and chicks than pairs nesting inland. Reproductive success in two years of study was higher at coastal nests than at inland nests. We suggest that the differences in spacing between the two sites may be due to different predator populations at the two sites. *Received 26 June 1992, accepted 23 Jan. 1993.*

Spacing patterns of nesting precocial birds have probably evolved to exploit food resources efficiently or to thwart predators (Hamilton 1971, Goransson et al. 1975, Safriel 1975, Page et al. 1983, Village 1983, Picman 1988). Phenotypic plasticity in spacing behavior likely results from differences in the intensity of predation and/or differences in the importance of food in different localities. In addition, a number of abiotic effects might explain differences in the spacing patterns among populations of a single species. For example, larger nesting aggregations might result simply because there is less nesting habitat for a similar number of birds between sites, resulting in more clumped spacing patterns and also higher densities of birds (Village 1983). Hiding places for the young may be more restricted at one site, and as a result, birds must nest in large aggregations and/or at higher densities to use these more restricted resources. Finally, climatic conditions may favor aggregative behavior if, for example, one site becomes available earlier than another, affecting the amount of available habitat through time.

Semipalmated Plovers (*Charadrius semipalmatus*) nest on flat, sparsely vegetated habitats in the Arctic (Hantzsch 1929, Soper 1946, Sutton and Parmelee 1955). In and around Churchill, Manitoba, this species nests in small aggregations or as single pairs at locations away from the coast (inland) and in larger aggregations on beaches directly adjacent to the coast. This variation in spacing patterns was documented in different

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geographical areas in earlier studies (e.g., "neighborhood" in Labrador [Hantzsch 1929] solitary breeding pairs in southwestern Baffin Island [Soper 1946] "close-knit group . . . colony" in southeastern Baffin Island [Sutton and Parmelee 1955], but has not been documented within a relatively small geographical area. Herein, we test whether nest availability, hiding place availability for chicks, or climate differences explain differences in spacing patterns of this species in the Churchill area. We also document differences in reproductive ecology, predator populations and reproductive success between coastal and inland locations.

STUDY AREA AND METHODS

This study was conducted from 12 June to 1 August 1987 and 31 May to 8 August 1988 in and around Churchill, Manitoba (58°45'N, 95°04'W). The study sites were divided into two areas: coastal, where birds nested along the coast of Hudson's Bay in gravel areas encircled by tundra vegetation or willows (*Salix* spp.) on three sides and the coast on the fourth; and 'inland' where birds nested in gravel areas mostly surrounded by scattered white spruce (*Picea alba*), larch (*Larix laricina*), willows (*Salix* spp.) and junipers (*Juniperus communis* var. *depressa*), and far enough from the coast so the chicks were not seen to move to the coast until they could fly. At the coast parents and chicks moved away from the nesting areas to adjacent mudflats to feed, whereas inland, parents led the chicks to the edges of nearby freshwater ponds to feed. Preliminary observations of spacing patterns, nest initiation dates, clutch sizes, and egg sizes were made in the 1987 field season. Nest initiation dates were estimated by back-dating from the date of hatch, using an incubation period of 26 days (this study).

In 1988, all nests but one were found during the egg-laying period. Most nests were found on gravel with small (<1 cm) pebbles, although one inland nest was on lichens, and one coastal nest was on sand. The entire Churchill area accessible by bicycle was surveyed for potential nesting areas. All gravel areas were considered to be potential nesting areas. Sizes of nesting areas were obtained by assuming a rectangular shape and measuring the longest and widest points (minus the areas of ponds). Small rocks and sparse vegetation were ignored. Densities were calculated as the number of pairs divided by the area of gravel (ha) in which that pair was found. Nearest-neighbor distances were calculated for coastal birds only, as all 'inland' birds nested alone or greater than 50 m from another pair. Nest sites at each study area were checked every day before and during laying and hatching. During incubation, nests were checked from a distance of 10 m or more, for the presence of the incubating adult, at least every three days. Semipalmated Plovers did not begin incubating until clutch completion.

In nests where the laying order was known, eggs were numbered with indelible felt-tip markers, weighed to the nearest 0.1 g, and measured to the nearest 1 mm. For virtually all nests in 1988, fresh egg masses were obtained. At hatching, chicks were weighed and banded with a numbered aluminum band.

Air temperatures were taken in the open with a thermometer at (1) 1 cm above ground level, (2) 3 cm above ground level, the approximate height at which a Semipalmated Plover sits while incubating, (3) 0.5 m above the incubating bird, and (4) 1 m above the incubating bird. We frequently recorded temperature in the large gravel areas over the breeding season, from 1 June to 8 August 1988. Wind speed readings were also measured with an anemometer at these heights.

RESULTS

Nest dispersion patterns.—In 1987, we found six nests inland and six nests along the coast. Three inland nests were in separate gravel areas, while three were on one very large gravel area but widely spaced (>50 m apart). Five of the six coastal nests were together on one gravel area. In 1988, the 20 pairs that we found at the coast were all nesting in one of four gravel areas. The 28 inland pairs were in 25 separate gravel areas. Twenty-two pairs nested solitarily, and six nested on the three largest gravel expanses. Nearest neighbor distances at the coast, averaged 16.5 m (SE = 3.36). All inland nests were at least 50 m from the nearest nest, including the seven pairs that nested on the three largest gravel areas. Nearest-neighbor distances were significantly smaller than 50 m at the coast ($t = 19.9$, N = 22, $P < 0.0001$).

The frequency distribution of pairs per area in 1988 deviated significantly from the Poisson distribution (categories for 5, 6, and 7 pairs per gravel area collapsed for analysis, Fig. 1, adj. G = 7.95, $P < 0.05$; $\chi^2 = 14.1$, 3 df, $P < 0.05$). The largest deviation came from the 22 pairs that nested solitarily at inland locations (Fig. 1). The distribution of pairs nesting at inland locations among gravel areas was significantly uniform (I = 0.098, N = 25, $\chi^2 = 2.35$, Elliot 1977), while the distribution of pairs among the four locations at the coast did not differ from random (I = 0.40, N = 4, $\chi^2 = 1.6$).

Availability of nesting habitat.—The areal extent of the gravel both on the coast and inland varied widely. There were 67.6 ha of available habitat on the coast and 114.8 ha inland. The median area of the coastal sites was not significantly different from that available inland (Table 1), and there was considerable overlap in the size of areas available at the two locations (Table 1). The difference in nest dispersion between the two sites did not appear to be due to having only small areas available inland and large areas available at the coast.

By calculating the densities of each area separately, we found that nesting densities were also not significantly different between the two sites (Table 1). The total number of pairs per total gravel area was lower on the coast than inland (coast, 0.30 birds/ha; inland, 1.89 birds/ha). Therefore, uniform spacing at inland sites was also not a function of having fewer birds per inland area.

Hiding sites.—At inland sites, parents led chicks to feed along the edges of inland ponds. At the coast, chicks foraged on the intertidal mudflats. Low vegetation surrounding feeding areas was dense at both inland and coastal locations and provided hiding places for plover chicks. Distances from the mudflats to the vegetation were not significantly different be-
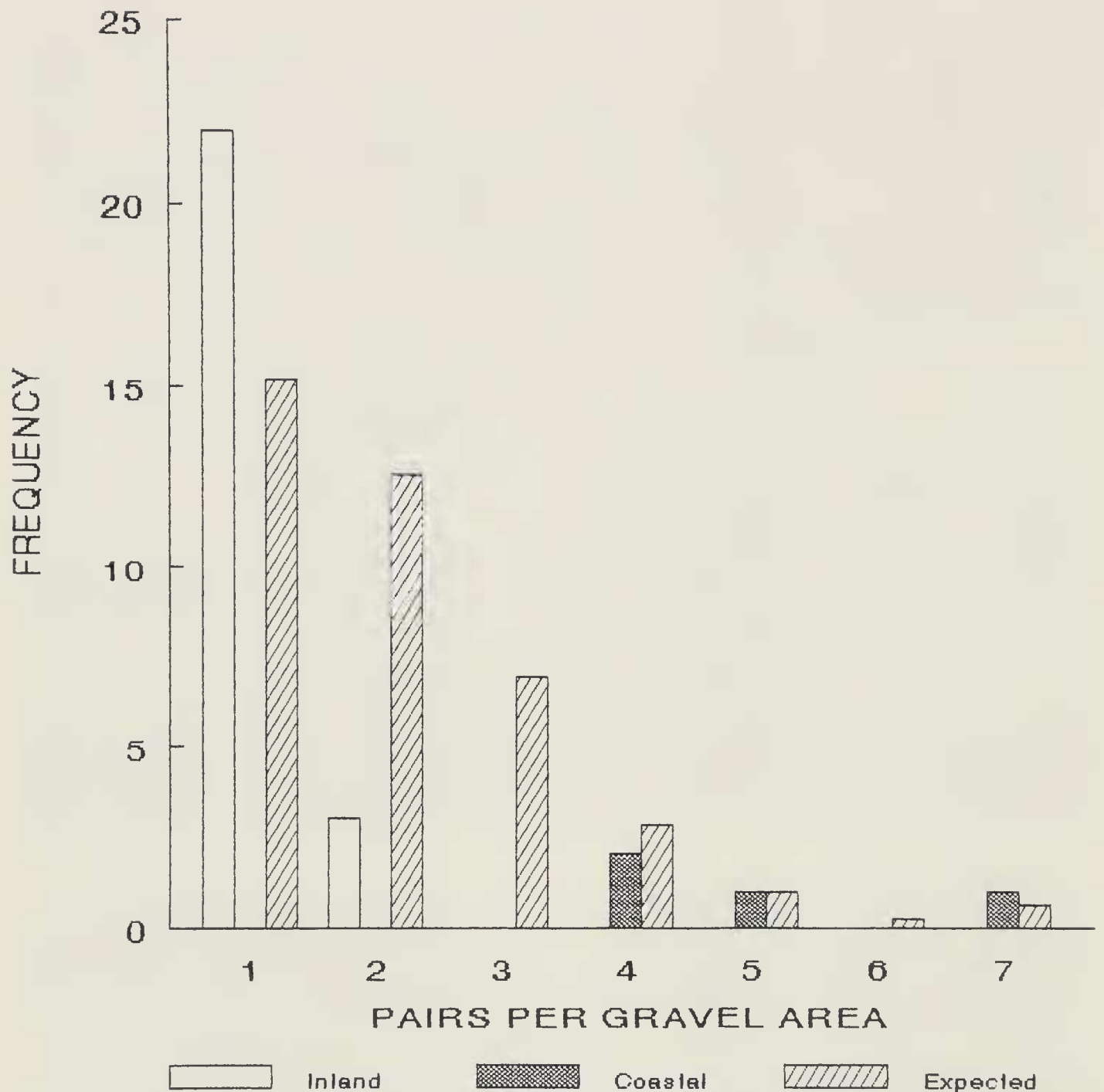
FIG. 1. Frequency distribution of number of pairs per gravel area from the 1988 field season, showing observed and expected numbers (based on a Poisson distribution).

tween the two sites ($t = 0.24$, coast: $\bar{x}$ + SE, 3.12 ± 0.700 m; inland 2.92 $\pm$ 0.324 m). Therefore, we also reject the hypothesis that birds on the coast are exploiting more restricted areas for hiding.

Climate. — To analyze the temperature data, we divided the 1988 season into four equal parts (1 June–15 June, 16 June–30 June, 1 July–15 July, 16 July–31 July). We then compared the temperatures at the four heights in four equal quarters of the day. Early in the season (1 June–15 June), temperatures were generally higher inland than at the coast, but only at heights greater than 0.5 m above the level of the bird, and only between 03:00 and 09:00 h CDT (e.g., at 0.5 m above the incubating bird). Mean temperature at the coast was 1.92°C (SE = 4.85, N = 4) and inland was

TABLE 1
NEST DENSITIES AND SIZE OF GRAVEL AREAS AT INLAND AND COASTAL STUDY AREAS IN 1988

	N	Coast median (Range)	N	Inland median (Range)	P^a
Nesting densities (pairs/ha)	4	0.36 (0.01–4.00)	23	1.26 (0.03–140)	0.357
Size of gravel area (ha)	4	12.9 (1.0–647.9)	23	0.79 (0.007–28.7)	0.071

[a] Significance determined using Mann-Whitney U-test.

9.69°C (SE = 1.36, N = 12). In no other comparisons (total of 64) were temperatures at any height significantly lower (or higher) at the coast than inland. Windspeeds were generally higher at the coast, but at the heights of the incubating bird and at ground level the differences were significant for only about half of the readings (e.g., 1 June–15 June, 15:00–21:00, coast, 2.98 ± 0.61 kph, N = 14, inland, 0.93 ± 0.13 kph, N = 13, t = 3.31, P = 0.005). As most coastal nests were behind low (<1 m) dunes, these nests did not experience offshore winds directly. As the greater winds of the coast did not correlate with lower hatching success at the coast (see below), we reject climate as an explanation for differences in spatial distributions between the two sites.

Reproductive ecology at inland and coastal locations. — In 1987, plovers had arrived on the study area before our field work began (12 June). In 1988, Semipalmated Plovers began arriving in Churchill on 2 June and dispersed onto territories and began nesting on 5 June. We found no significant differences in the date of clutch initiation between coastal and inland nests in 1987 (Table 2). In 1988, however, there was a significant difference in egg-laying dates between the coast and inland, with females at the coast laying eggs an average of three days later than the females at inland sites (Table 2).

In 1987, all nests contained four eggs. In 1988, 26 of the inland nests contained four eggs, one contained three eggs, and one contained two eggs. All 20 coastal nests contained four eggs. In 1987, there was no evidence that eggs at the two locations were significantly different in volume or mass (Table 2). In 1988, eggs and chicks from coastal nests were significantly heavier than eggs and chicks from inland nests, but eggs had significantly smaller volumes (Table 2). Fresh egg mass and fresh chick mass were significantly correlated (N = 123, r = 0.49, P < 0.01; Ricklefs 1984). We tested for the added variance component for the egg parameters,

TABLE 2

DIMENSIONS, VOLUME, AND MASS OF EGGS AND FRESHLY HATCHED CHICKS FROM COASTAL AND INLAND LOCATIONS NEAR CHURCHILL, MANITOBA

Year	Parameter	N[a]	Inland $\bar{x}$ (SE)	N	Coastal $\bar{x}$ (SE)	P
1987	Egg length, mm	6	31.7 (0.37)	6	31.4 (0.25)	n.s.[b]
	Egg breadth, mm	6	22.5 (0.09)	6	22.5 (0.24)	n.s.
	Egg mass, g	6	9.6 (0.35)	6	9.9 (0.29)	n.s.
	Egg volume, cm³	6	6.78 (0.084)	6	6.73 (0.130)	n.s.
	Laying date	6	12 June (1.1)	6	11 June (1.3)	n.s.
1988	Egg length, mm	28	32.7 (0.26)	20	31.9 (0.22)	0.029
	Egg width, mm	28	23.0 (0.13)	20	22.5 (0.12)	0.012
	Egg mass, g	28	8.3 (0.10)	20	9.2 (0.12)	0.0001
	Egg volume, cm³	28	7.3 (0.12)	20	6.8 (0.11)	0.003
	Chick mass, g	16	6.0 (0.14)	17	7.1 (0.14)	0.0001
	Laying date	28	14 June (0.61)	20	17 June (0.56)	0.0003

[a] Sample size is based on number of nests (means for each nest were analyzed).
[b] n.s. = means not significant.

once the effects of location had been removed (SAS Institute 1985). There were significant added variance components (or differences among females) for egg volume, egg length and egg breadth, (66.9%, $F_{46,140} = 8.91$, $P < 0.01$; 72.6%, $F_{46,140} = 11.41$, $P < 0.01$; 58.6%, $F_{46,140} = 6.54$, $P < 0.01$, respectively) but not for egg mass (13.5%, $F_{46,140} = 1.61$, n.s.).

Predation and reproductive success.—A number of potential predators including Rough-legged Hawks (*Buteo lagopus*), Prairie Falcons (*Falco mexicanus*), Parasitic Jaegers (*Stercorarius parasiticus*), Herring Gulls (*Larus argentatus*), Common Ravens (*Corvus corax*), Arctic foxes (*Alopex lagopus*), red foxes (*Vulpes vulpes*) and ermines (*Mustela erminea*) were seen during observations at nest sites, but mammalian predators were observed only at inland sites. Over both years the number of nests where at least one egg hatched was significantly higher at the coast than inland (Table 3). In 1988, nearly one half of all inland nests were unsuccessful in hatching (Table 3), whereas in both years most coastal nests hatched successfully. In 1987, six nests contained one egg that did not hatch (4 at coast, 2 inland). In 1988, five inland nests experienced partial nest loss (4 pairs lost 1 egg, 1 pair lost 2 eggs).

DISCUSSION

Evidence does not support the hypotheses that differences in spacing at coastal and inland locations are due to less available nesting habitat at the coast than inland, higher densities at the coast than inland, smaller

TABLE 3
HATCHING SUCCESS OF COASTAL AND INLAND NESTS

Year	Location	Successful	Unsuccessful	P^a
1987	Coast	6	0	0.439
	Inland	4	2	
	Coast	17	3	0.098
1988	Inland	17	12	

[a] Using likelihood ratio, continuity-adjusted chi-square. When data from the two years are combined, the difference between locations is significant at $P = 0.031$.

patches of available habitat, better hiding places at the coast than inland, or more favorable climate at the coast than inland. Our data on nest densities, available habitat, and the distribution of pairs per area suggest that the pairs at each location are distributing themselves differently in space in response to biotic rather than abiotic factors.

Predation is probably one of the most important selective pressures influencing the optimal spacing pattern of a population (Andersson and Wiklund 1978, Page et al. 1983, Picman 1988). Several experiments have shown that predation on cryptic prey nesting in open habitats increased with prey density (Tinbergen et al. 1967, Krebs 1971, Page et al. 1983). Therefore, predation seems to favor spacing out by prey whose main defense is to avoid detection.

However, in species that communally act against the threat of a predator, defense efficiency may increase with the number of defenders (Tinbergen et al. 1967, Andersson and Wiklund 1978, Underwood 1982, McLandress 1983). This would favor higher prey densities or clumping. Since both solitary nesting and clumping are observed in the Semipalmated Plover, it may be possible that different patterns are advantageous at the different sites.

No foxes were ever seen at the coast, but foxes and other mammalian predators were observed on numerous occasions near inland nests, probably because inland sites provided hiding and denning places (Banfield 1974). Foxes were likely important predators at these sites. Although aerial predators were often seen flying over nests, plovers rarely left the nest as a result. The usual response was to go into a crouched position and wait for the threat to pass, presumably relying on their highly cryptic plumage to avoid detection (Page et al. 1983).

Low densities of Snowy Plovers (*C. alexandrinus*) at Mono Lake (Page et al. 1983, within the ranges of density found at either of our sites) were suggested to function as important anti-predator responses against ravens

and gulls. We found that clumping occurred at the site where only avian predators were observed, although avian as well as mammalian predators occurred at the inland sites where birds were spaced out in their distribution. It may be that only the significant 'spacing out' or uniform distribution of the inland birds can be seen as an anti-predator response to predators at inland sites (i.e., Picman 1988). It remains to be determined why the birds at the coast 'clumped.'

We observed differences in the effect of the anti-predator response of plovers to our presence at the two locations. When inland nests were approached, the birds skulked off the nest toward the observer and performed a broken-wing display. The same behavior was seen at the coast, but because more than one nest was nearby, up to nine birds could be calling and displaying simultaneously, presumably confusing potential predators.

Hatching success was significantly higher at the coast than inland and very high (100% in 1987, 85% in 1988), as compared to hatching success of some other plover populations (Nol and Lambert 1984, Page et al. 1985, Haig and Oring 1988, but see Wilcox 1959, Cairns 1982). The advantages ascribed to 'spacing out' for cryptic species suggest that if predators 'discovered' one of the clumped nests, substantial losses would occur. However, three nests were lost in 1988 from three different coastal locations. Therefore, crypticity of eggs and/or group defense (Skeel 1983) must be affording the coastal birds some protection. The relatively low density of birds at the coast in relation to available habitat suggests that these birds may have been 'hiding in a sea of gravel.'

The differences in spacing patterns between these two geographically close locations does not explain why individual birds would choose to nest at one location over the other. Inland birds began nesting three days earlier than coastal birds, but we had no evidence that either habitat was preferred or saturated. At the larger inland areas and at all coastal sites, there appeared to be sufficient available habitat to increase the number of pairs further. In addition, we did not see any overt territorial behavior at coastal sites, that might imply nest-site limitation, despite the nearness of nests. However, snow left the coastal areas later than inland sites in 1988.

Adults were often observed flying between the two sites to forage, so it was unlikely that food availability for the laying females resulted in differences in egg and chick size between the two locations or in differences in spacing behavior. If the earlier availability of nest sites is the reason for the difference in egg mass between the two sites, then one would expect no differences in egg mass between the two sites in 1987, when there were no differences in laying dates. In addition, we found that the added vari-

ance component for egg mass was very small when compared to the added variance component for volume and linear egg dimensions. This suggests that egg mass is affected more strongly by environmental changes than is volume (Ricklefs 1984). It is possible, however, that food availability for the chicks varies between the two sites and that lower food availability at inland sites leads to more territorial behavior, hence spacing out at these locations. Currently, we do not have information to test this hypothesis.

Differences in spacing behavior within a species of precocial bird because of predators and/or food availability for chicks may have important implications for patterns of parental behavior (Walters 1982). The effects of these differences between coastal and inland sites on parental behavior in this species are currently under study.

ACKNOWLEDGMENTS

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